

Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularity

Aniek A. Schoups, Rufin Vogels and Guy A. Orban

Laboratory of Neuro- and Psychophysiology, K.U. Leuven, Campus Gasthuisberg, B-3000 Leuven, Belgium

1. Human perceptual learning in discrimination of the oblique orientation was studied using psychophysical methods. Subjects were trained daily to improve their ability to identify the orientation of a circular 2.5 deg diameter unidimensional noise field. Dramatic improvements in sensitivity to contour orientation occurred over a period of 15–20 days. The improved performance persisted for several months. Improvement was more evident between daily sessions than within sessions. This was partly due to fatigue interfering with the learning effect. Moreover, a consolidation period seemed to be required.
2. Improvement was restricted to the position of the stimulus being trained. This position dependency of the learning effect proved very precise. After training at a specific stimulus position, merely displacing the stimulus to an adjacent position caused a marked increase in thresholds.
3. No transfer of the training effect was observed between orientations. Following a shift of 90 deg away from the trained orientation, performance fell, even below the initial level.
4. We observed complete to almost complete transfer between the two eyes.
5. Our results suggest plastic changes at a level of the visual processing stream where input from both eyes has come together, but where generalization for spatial localization and orientation has not yet occurred.

Improvement in perceptual judgement with training is a form of adult plasticity that can easily be studied in the human. It has been observed in virtually all sensory modalities and, when a genuine increase in sensitivity is demonstrated, it is called perceptual learning (Gibson, 1953). In the somatosensory and auditory system, Recanzone, Schreiner & Merzenich (1993) have demonstrated that tactile and auditory discriminative abilities improve with practice, and that these behavioural changes are correlated with neuronal changes. In the visual system, performance in several visual tasks is known to improve dramatically with practice: perceptual learning has been observed in discriminations of various visual features, including global stereopsis (Ramachandran, 1976), spatial phase (Fiorentini & Berardi, 1981; Berardi & Fiorentini, 1987), direction of motion (Ball & Sekuler, 1987), texture (Karni & Sagi, 1993), stereoacuity (Fendick & Westheimer, 1983) and hyperacuity (McKee & Westheimer, 1978; Fahle & Edelman, 1993).

Perceptual learning has also been observed in two studies on line orientation discrimination (Vogels & Orban, 1985; Shiu & Pashler, 1992). However, the mechanism and the

localization of this form of adult plasticity in the visual system remain largely unknown. A learning effect specific to the retinal position would imply that the mechanisms involved are active over a limited area of the visual field. Shiu & Pashler (1992) investigated the position dependency of the learning effect, but only in a rather coarse fashion: improvement for a stimulus positioned in one corner of the subject's visual field (at 8 deg eccentricity) did not transfer to a stimulus positioned in the other corner. Thus, no transfer occurred across hemifields or across quadrants in the same hemifield. A precise localization of the learning effect in the visual system cannot be derived from these data since retinotopy is conserved, not only in area V1 and V2, but even, at least coarsely, up to area TEO (Boussaoud, Desimone & Ungerleider, 1991). Neurons at lower levels in the visual processing stream have much smaller receptive fields than cells in the higher visual areas, and these lower visual areas therefore map the visual world in very fine detail. The precision of the retinotopy, rather than the retinotopy itself, will be relevant in the localization of the learning effect. Similarly, much information can be gathered from studying the orientation specificity of the learning effect.

Early in the visual pathway, different orientations are handled by independent 'channels' (Hubel & Wiesel, 1968; Blakemore & Campbell, 1969), such that the learning that occurs will most probably be associated with one orientation without development of an equivalent association with the orthogonal orientation. Both Shiu & Pashler (1992) and Vogels & Orban (1985) investigated the orientation specificity of the learned improvement in line orientation discrimination. The former study observed a decrease in performance after a change in orientation markedly below the initial level of performance. In contrast, Vogels & Orban (1985) noticed that performance for the non-practised orientation had improved during the training schedule, though not as much as for the practised orientation. The importance of position dependence and orientation specificity in the determination of the localization of this form of adult plasticity in the visual system led us to re-examine perceptual learning in orientation discrimination. Finally, the specificity of the learning effect for the trained eye can also provide information on the anatomical locus of the learning. By comparing the receptive field size and precision of the position dependency, together with the orientation specificity, we hoped to determine the upper limit for localization of the learning effect in the visual pathway. On the other hand, since monocular cells can be found only in cortical area V1 (Hubel & Wiesel, 1977), any restriction in the improvement of the eye with training would unequivocally point to the primary visual cortex as the site of the anatomical changes. This would enable us to set the lower limit for the localization.

The aim of our study was therefore to investigate, firstly, whether improvement in performance for a particular stimulus location in the visual field would transfer to a nearby stimulus position. We tested various positions in the visual field, both between the hemispheres and within the same quadrant. We were especially interested in the minimum distance between the trained and the new position required for a rise in the threshold. Secondly, we studied whether practising one orientation would confer a gain to the identification of another orientation, and thirdly, we investigated the monocularity of the learning mechanism. We decided to use a circular unidimensional noise field for the stimulus, containing a set of spatial frequencies, instead of the single line used in previous studies (Vogels & Orban, 1985; Shiu & Pashler, 1992). This enabled us to maximize the number of neurons involved in the task. Moreover, when combined with phase randomization of the various stimuli presented, we could remove any position cues that would help in solving the orientation identification task. Preliminary data have been presented in abstract form (Schoups, Vogels & Orban, 1993).

METHODS

Six subjects (A.C., A.S., C.S., G.M., I.S. and K.L.; five females and one male), without previous experience in psychophysical orientation discrimination tests, participated in the experiment. They had normal or corrected-to-normal eyesight. For those subjects participating in monocular tests, both eyes did not differ from one another by more than 0.25 dioptres. The heads of the subjects were not restrained and they viewed the stimuli in a dimly lit room (0.007 cd m^{-2}).

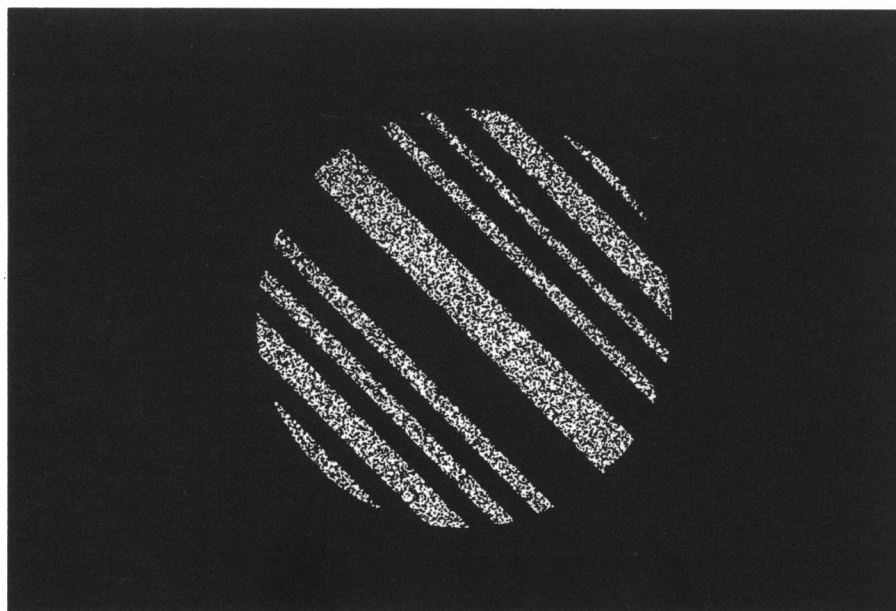


Figure 1. Example of a stimulus used in the experiments

The width of the bars and their position varied randomly between different stimuli, i.e. between trials.

The stimulus was a circular 2.5 deg diameter unidimensional noise field, consisting of light and dark bars (Fig. 1). The width of these bars varied randomly from 0.077 to 0.312 deg. The light bars contained randomly positioned white and black pixels, and had a mean luminance of 2.5 cd m⁻². The dark bars (where all pixels were black) and the background had a luminance of 0.090 cd m⁻², thus resulting in a Michelson contrast ratio between light and dark bars of 93%. The noise field was made up of a set of spatial frequencies (ranging between 1.6 and 6.5 cycles deg⁻¹) of which the relative phases were randomized over the trials. The stimuli were displayed on an ATRIS monochrome monitor (resolution, 1440 × 728 pixels; frame refresh rate, 77 Hz; ETAP, Malle, Belgium). Intertrial interval was 1 s and stimulus exposure time was 300 ms. Subjects had to respond within 600 ms of stimulus onset. A light-emitting diode was used as the fixation target. Stimuli were positioned centrally, at 5 deg eccentricity and at 7.9 deg eccentricity.

The subjects practised orientation discrimination at only one reference orientation, the left oblique standard orientation. We chose this orientation because we expected more learning to occur with an oblique orientation than with a horizontal or vertical orientation. Indeed, an earlier study on line orientation discrimination reported that while selective practice of the oblique standard orientation decreased its threshold by a factor of 1.9, practising a principal standard orientation yielded no reduction in just noticeable difference (JND) (Vogels & Orban, 1985). In identifying the orientation of a line tilted 9.8 or 7 deg counter-clockwise from the vertical, only a 10% increase in accuracy was observed (Shiu & Pashler, 1992). However, the latter study used very short lines (and an eccentricity of 8 deg), making the task very difficult, and the subjects were not prevented from using position cues (Orban, Vandenbussche & Vogels, 1984). In our study the stimulus was designed so that the subjects could not use a cue other than orientation to solve the task.

The task was one of identification (Vogels & Orban, 1985), only one orientation being presented in each trial. The subjects had to decide whether the noise field was tilted clockwise or counter-clockwise to the reference orientation. Auditory feedback was provided.

We used a transformed up-down staircase procedure (Wetherill & Levitt, 1965) which converged on an orientation difference corresponding to an 84% correct criterion. In this procedure the reference orientation was never presented. The difference between the orientation of the bars and the reference oblique orientation was called the orientation difference (δ). The starting value for δ was 7 deg. Step size was set at 20% δ . JNDs were defined as the logarithmic mean of the reversal points obtained during 100 trials. Daily sessions consisted of sixteen blocks of 100 trials, except for the monocular testing, where sessions comprised only ten blocks of 100 trials. The geometric mean of these ten or sixteen JNDs was determined. Subjects were trained until asymptotic performance was reached over six sessions.

When investigating the retinotopy of the learning effect, a method of single stimuli (MSS) was also used (Vogels & Orban, 1986). The orientation difference δ at which the subject reached a 90% correct criterion was split into three equal parts. This was done at either side of the oblique. Thus, one of seven possible orientations at symmetrical intervals around the reference orientation, and including it, was presented. As in the staircase method, there were two response alternatives. The orientations were presented in random order, and with equal frequency. The data of the 1600 trials obtained over the whole session were pooled, and the proportion of left-key responses was calculated for each orientation. After z-normalization of these proportions and linear regression, the 84% correct JND was given by the standard deviation. This method also offered an opportunity to determine the point of subjective equality (PSE), thus estimating the subject's bias during these tests. The PSE was given by the orientation at which the subject responded with either key with

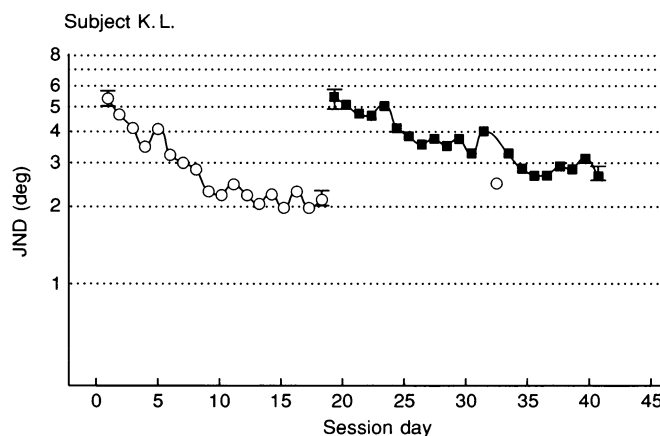


Figure 2. Learning curve for orientation discrimination for a central stimulus and the same stimulus presented at 5 deg eccentricity

Median JNDs obtained over 16 blocks (except in a few sessions where only 9 or 10 blocks were performed) of 100 trials per day, are plotted as a function of the number of previous sessions. The subject (K.L.) was trained binocularly with the staircase procedure. Performance for the centrally presented noise field was retested 3 weeks after training at the peripheral position. The upper and lower quartile boundaries (25th and 75th percentile) are indicated for the first and last training day at each position. ○, central stimulus; ■, the same stimulus at 5 deg eccentricity.

equal probability. Comparison of the thresholds obtained from the staircase method and the method of single stimuli indicated that the subjects used an 'absolute identification rule', and not a 'paired comparison rule' when solving the task (Vogels & Orban, 1986).

RESULTS

Perceptual learning in orientation discrimination

All subjects improved their performance in the orientation discrimination task. Figure 2 shows a typical perceptual learning curve, obtained by plotting the daily median JND as a function of the number of sessions. This subject, K.L., was binocularly tested and trained to discriminate orientation around the left oblique for a central stimulus and subsequently for the same stimulus located at 5 deg eccentricity. Variability within each session was small, as is evident from the upper and lower quartile boundaries indicated for the first and last training day at each position (Fig. 2). When threshold was reached, the effects of learning remained for at least 3 weeks, as was evident from retesting the previously trained central position (Fig. 2). Similar learning curves were obtained when testing other subjects who were trained at various stimulus positions in the visual field. We calculated the effect of training on each subject, for all the positions binocularly trained at 5 deg eccentricity.

The difference between the JNDs obtained during the first day of training at one position and the last day of training at that position was highly significant (subject A.C., 2-way ANOVA with three positions, $F(1,13) = 80.53$, $P < 0.000001$; A.S., 2-way ANOVA with three positions, $F(1,15) = 97.95$, $P < 0.000001$; K.L., 1-way ANOVA with one position, $F(1,8) = 91.74$, $P < 0.00001$). Through training, JNDs decreased by a factor of 1.4 for the position at which the least learning was observed, to a factor of 4.3 for the position at which the largest improvement in performance was observed.

The effect of training can also be illustrated by determining the across-subject mean JND at the start and end of training at a particular position. These JNDs are shown in Fig. 3 for a central stimulus and for one stimulus position at 5 deg eccentricity.

As for the time course of improvement over the various sessions, learning was always fast initially, but levelled off after five to ten sessions, such that $90 \pm 3\%$ of the improvement occurred during these first ten daily sessions. Table 1 gives an overview of the improvement as measured during these first ten sessions, for all subjects and all positions. Again, improvement is demonstrated by the difference in JND at the start of the training and after the tenth session (Table 1, first three columns). Improvement was also evident from the significantly negative slopes of the regression lines through the first ten

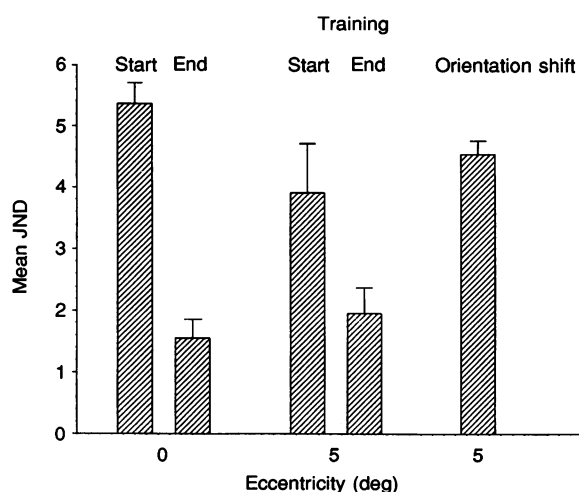


Figure 3. Effect of training on the orientation discrimination thresholds for a central stimulus and a stimulus at 5 deg eccentricity: dependency of position and orientation

Three subjects were trained binocularly at 0 and 5 deg eccentricity around the left oblique orientation (135 deg). The orientation of the noise field was then shifted 90 deg. Daily sessions consisted of 16 blocks of 100 trials of staircase procedure, from which the geometric mean JND was determined. Across-subject mean JNDs at the start of training are based on the median JNDs of the subjects' first day of training at that stimulus position. Across-subject mean JNDs at the end of the training are based on the asymptotic level reached during the last 6 training sessions at that stimulus position. Mean JNDs for the shifted oblique orientation (45 deg) are based on the median JNDs from the first day of testing with this untrained oblique orientation (at the same position as the trained orientation). Error bars represent s.e.m. across the 3 subjects.

sessions (Table 1, last three columns). The variability in steepness of the learning curve was due to inter-individual differences, and to previous experience in learning the orientation discrimination task. The largest improvement was observed in completely inexperienced subjects, for whom learning the task constituted an initial impediment before perceptual improvement could occur.

Specificity of the learning effect

Retinotopy

Investigating the specificity of the learning effect, we focussed initially on whether the effect of training is retinotopic. This issue consisted of two main questions. Firstly, is the improvement in performance gained over the training sessions restricted to the stimulated region of the visual field? Secondly, how precise is this retinotopy, and how far apart need a trained and a new position be for new learning to be required?

It soon became evident that the learning effect was indeed specific for the position in the visual field. Figure 4 shows the retinotopy of the learning effect, as well as its

precision, tested with subjects A.C. and A.S. Both subjects were first binocularly trained for the task with a stimulus presented centrally, and subsequently tested and trained at eight different positions at 5 deg eccentricity (Fig. 4A). The staircase procedure was used for all training and testing of subject A.C., and for positions 1 to 4 of subject A.S. For each stimulus position, the subject's performance improved with practice. Variability within each session was as small as in Fig. 2, and is, for the sake of clarity, not indicated in the learning curves shown in Fig. 4B and C. After displacement of the stimulus to a different position, no transfer of the learning effect to the new position was observed. Indeed, JNDs obtained at a new position were always well above asymptotic performance of the trained position; the difference between the JND of the last training day at one position and the JND of the first training day at the next position was always highly significant (using a 2-way ANOVA with three positions, results for A.C. were $F(1,11) = 41.8$, $P < 0.00005$; and for A.S., $F(1,15) = 77.9$, $P < 0.000001$; data for the central stimulus were not considered in the statistical analysis). This position

Table 1. Learning as measured during the first ten sessions: improvement and linear regression through the curves relating median JND to the number of sessions

		Improvement in median JND			Linear regression through 10 sessions		
Position *		At first session (a)	At tenth session (b)	Difference (a - b)	r^2	P	slope
Binocular							
Subject A.S.							
	0	5.92	1.50	4.42	0.776	0.000	-0.417
	1	3.20	1.92	1.28	0.793	0.000	-0.135
	2	2.93	1.28	1.65	0.593	0.007	-0.124
	3	1.78	1.26	0.52	0.849	0.000	-0.055
	4	2.27	1.50	0.77	0.510	0.016	-0.067
	5	2.45	1.74	0.71	0.465	0.025	-0.058
	6	2.25	—	—	—	—	—
	7	2.10	—	—	—	—	—
Subject A.C.							
	0	4.78	1.32	3.46	0.760	0.001	-0.323
	6	2.70	1.82	0.88	0.901	0.000	-0.133
	2	2.52	1.57	0.95	0.764	0.000	-0.086
	2b	2.42	—	—	—	—	—
	4	3.05	1.61	1.44	0.616	0.005	-0.113
Subject K.L.							
	0	5.39	2.23	3.16	0.924	0.000	-0.325
	1	5.47	3.53	1.94	0.875	0.000	-0.215
Monocular							
Subject A.S.		5.15	2.98	2.17	0.677	0.002	-0.197
Subject I.S.		5.18	2.32	2.86	0.846	0.000	-0.292
Subject C.S.		4.17	2.12	2.05	0.525	0.014	-0.182
Subject G.M.		3.46	1.76	1.70	0.605	0.006	-0.158

* For binocular training, position 0 refers to the central stimulus. The other positions were at 5 deg eccentricity (see Fig. 4A). Monocular training was at 7.9 deg eccentricity for subject A.S., at 5 deg for I.S. and C.S., and centrally for subject G.M.

dependency of the learning effect proved to be very precise. The trained and new positions could be so close to one another that the surfaces of the stimuli were abutting but not overlapping (see Fig. 4).

Moreover, training at one side of the mid-line did not transfer to the other hemisphere. The centres of positions 2 and 3, and positions 5 and 6 (Fig. 4A) were 5.8 deg apart from one another. Thus, there was no interhemispheric transfer of the learning effect for stimuli whose outer limits were as close as 1.6 deg away from the vertical meridian.

It could be argued that the different positions in the visual field, though at the same eccentricity, may not be identical for performance at the orientation discrimination

task. This could explain the drop in performance upon a shift in stimulus position. However, for the two subjects that were extensively trained at various positions in the visual field (Fig. 4), the final thresholds obtained after extensive practice were the same for all stimulus positions. Indeed, no significant difference was observed among the JNDs at different positions when considering the last day of training (A.C., $F(2,30) = 2.84$, not significant (n.s.); A.S., $F(2,30) = 0.79$, n.s.). Moreover, when considering the first day of practice at each position, no effect of position on the JNDs was observed in one of the two subjects (A.C., $F(3,33) = 2.65$, n.s.). In the other subject there was a position effect (A.S., $F(3,45) = 13.2$, $P < 0.000003$). However, the difference was significant only for the first two positions, not for the positions

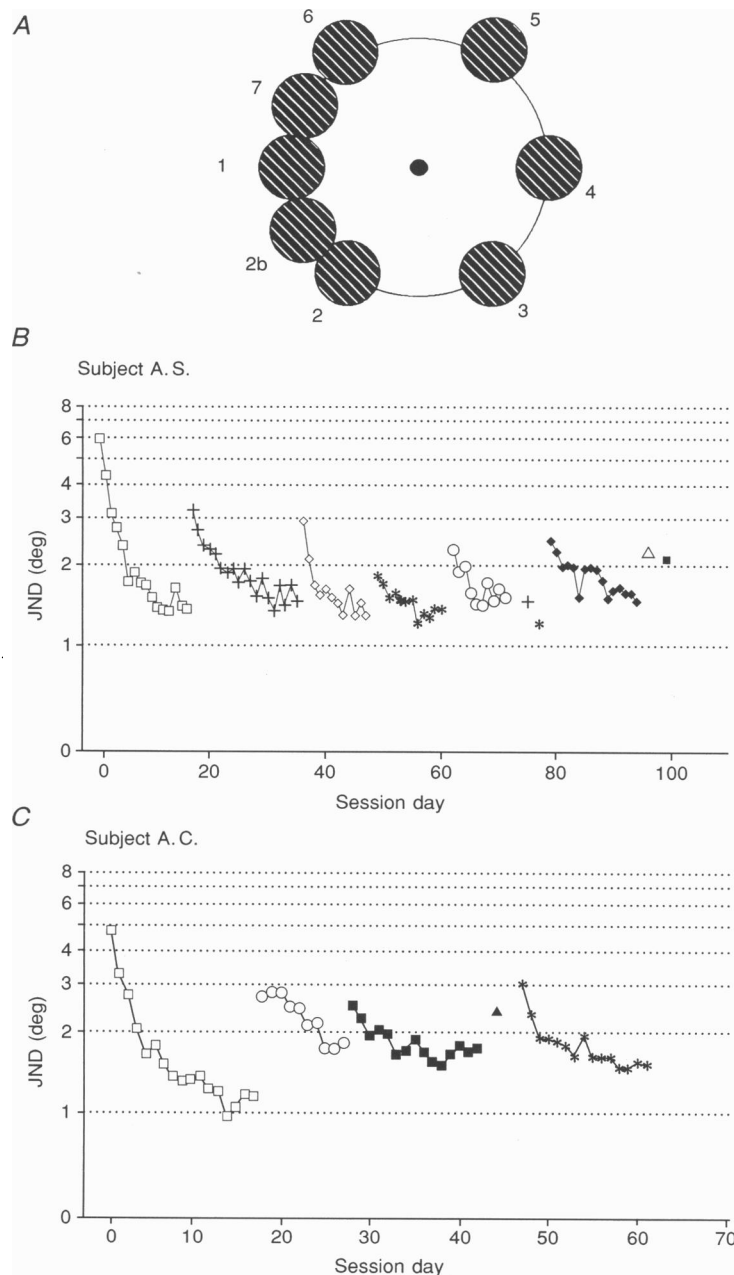


Figure 4. Retinotopy of the learning effect of two subjects with the retesting of previously trained positions

A, overview of the different positions for the noise field in the subject's visual field. The black dot in the centre represents the subject's fixation point. B, learning curves for subject A.S.

Orientation discrimination was first tested and trained at a central stimulus, then different positions at 5 deg eccentricity were tested and trained. Up to the last 3 days at position 4, the staircase method was used, whereas for positions 5, 6, 7 and the last 3 days at position 4, the method of single stimuli (MSS) was used.

Performance at position 1 was retested (with MSS) after training positions 2, 3 and 4; performance at position 3 was retested after training position 4. Positions 6 and 7 were only tested, and not practised further. □, foveal position; +, position 1; ◇, position 2; *, position 3; ○, position 4; ◆, position 5; △, position 6; ■, position 7; C, learning curves for subject A.C. Orientation discrimination was first tested and trained at a central stimulus, then 3 more positions were tested and trained, using the staircase method. Performance at position 2b was tested only, with no further practice. □, foveal position; ○, position 6; ■, position 2; *, position 4; ▲, position 2b.

trained thereafter. The effect therefore seems to be related to general experience with learning a task, especially since this subject was the most naive with respect to experience in psychophysical tests. Finally, two other subjects were each tested in one session at eleven new positions on a circle around the fixation point. Again, no difference in performance among positions became apparent (data not shown).

The retinotopy of the learning effect was further confirmed with the method of single stimuli (MSS). After subject A.S. had reached stable thresholds for orientation discrimination at position 4, three more testing days were performed using the MSS. JNDs from the MSS were identical to the threshold determined with the staircase procedure (Fig. 4).

The MSS was also used to demonstrate (1) the permanent, stable character of the threshold levels, as well as (2) the lack of bias effects on the subject's performance. (1) In six different sessions, performance at the previously trained positions 1, 3 and 4 was compared with performance at the new positions 5, 6 and 7. After z -transformation, the JNDs were determined by the standard deviation of the normalized distribution (Fig. 5). JNDs obtained for positions 1 and 3 remained unchanged, even though other positions had been trained in the meantime (see Fig. 4). Compared to the trained positions, new positions showed a significantly flatter slope of the psychometric curve (-0.456 ± 0.022 for positions 5, 6 and 7; -0.711 ± 0.036 for positions 1, 3 and 4), and thus a higher JND value (Fig. 5). (2) After this test, the subject continued to practise orientation discrimination at position 5 using the MSS. We calculated the point of subjective equality (PSE) determined while training subject A.S. at position 4 (last two training sessions) and 5 (all training sessions). Very little, if any, bias existed. When training the subject at position 5, the internal representation of the oblique never deviated more than 0.6 deg from the actual oblique (data not shown). The bias disappeared very quickly upon

further practice, and was gone after the fourth session, while the sensitivity required more sessions before improvement was seen (see Fig. 4).

Orientation specificity

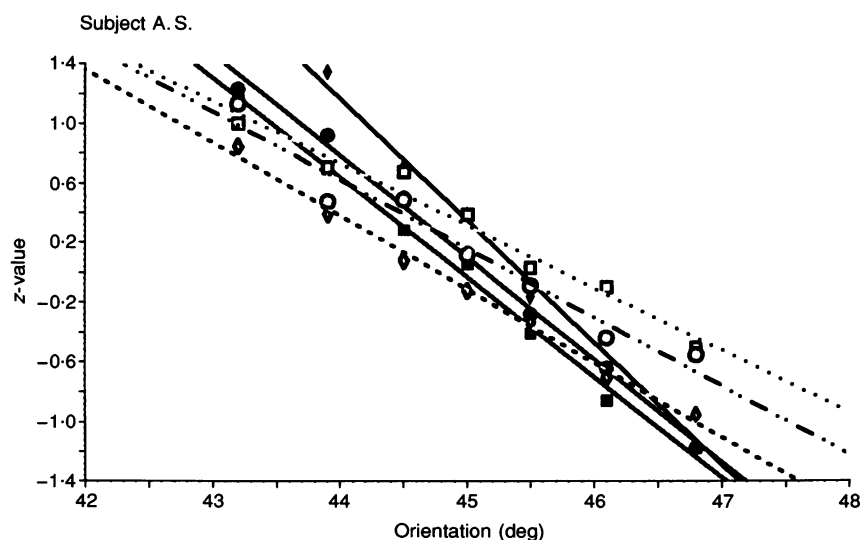
We investigated next whether the practice effect and the associated improvement in discriminative ability at a single orientation remained confined to that particular orientation. Previous work from our laboratory has shown that there is, on average, no difference in initial thresholds for the left or right oblique standard orientation (Vogels & Orban, 1985). Three subjects practised binocular orientation judgements around one oblique orientation, and were then tested on their ability to discriminate around the other oblique orientation, 90 deg away from the trained one (Fig. 6). The stimulus, presented at 5 deg eccentricity, was at the same position in the subject's visual field as the trained orientation. No transfer was observed between these orientations: within each subject the difference between the JNDs for the last day of training at one orientation and the JNDs for the other orientation upon first exposure was highly significant (A.C., $F(2,30) = 89.7$, $P < 0.000001$; A.S., $F(2,28) = 73.4$, $P < 0.000001$; K.L., $F(2,16) = 48.0$, $P < 0.000001$), as were the differences between the first and last day of training in one orientation (i.e. the effects of practice on one orientation). Further, compared with the pretraining JND for the practised orientation, performance for the new orientation was significantly worse for two out of three subjects (Fig. 6A and B). The absence of transfer between orientations is also illustrated by Fig. 3. This figure shows mean JNDs across the three subjects, at start and end of training around 135 deg at a peripheral position, and at their subsequent testing for the 45 deg orientation at the same position (Fig. 3).

Monocularity?

To further attempt to delineate the anatomical locus of the training effect, we tested whether transfer of training

Figure 5. Retinotopy of the learning effect tested with MSS

The method of single stimuli was used to compare performance at the already (with staircase) trained positions 1, 3 and 4 with performance at new positions 5, 6 and 7. \diamond , position 7 (new); \circ , position 6 (new); \square , position 5 (new); \bullet , position 1 (trained); \blacklozenge , position 3 (trained); \blacksquare , position 4 (trained).



between the trained and untrained eye would occur. Absence of interocular transfer would imply that the changes accompanying the learning remain restricted to monocular cells. Three subjects were tested on the first day for orientation judgements using either eye for a stimulus presented centrally (Fig. 7*D*) or at 5 deg eccentricity (Fig. 7*B* and *C*). They then continued to practise that orientation with one eye, while the other was covered with an opaque patch. A fourth subject (A.S., Fig. 7*A*) started practising one eye without previous exposure of the stimulus to the other eye; in her training protocol, the stimulus position was at 7.9 deg eccentricity. After reaching stable levels, the patch was switched to the untrained eye, and performance was again tested. In three subjects, complete transfer of the learning effect was observed between the two eyes (Fig. 7*A*, *B* and *D*). In these subjects, there was no difference between the trained eye on the last day of practice and the untrained eye tested on the following day. There was a highly significant effect of practice both for the trained and for the untrained eye

(A.S., $F(2,18) = 59.9$, $P < 0.000001$; G.M., $F(3,15) = 27.6$, $P < 0.000002$; I.S., $F(3,15) = 82.4$, $P < 0.000001$). In the fourth subject (C.S., Fig. 7*C*), transfer was only partial. For this subject, performance with the trained eye on the last day of training was still significantly above performance with the untrained eye. However, as in the other three subjects, practice had a highly significant effect on both the trained as well as the untrained eye ($F(3,15) = 51.3$, $P < 0.000001$). It is unclear why transfer was only partial in this subject, though probably the higher variability between sessions, especially around a stable threshold level, compared with the other subjects, accounts for this failure to observe complete transfer.

Is there improvement only within the training sessions?

We often found improvement within a daily session to be very small. To measure this improvement, we calculated the slope of the curve relating the JND to the number of blocks within a session. Figure 8 shows these daily

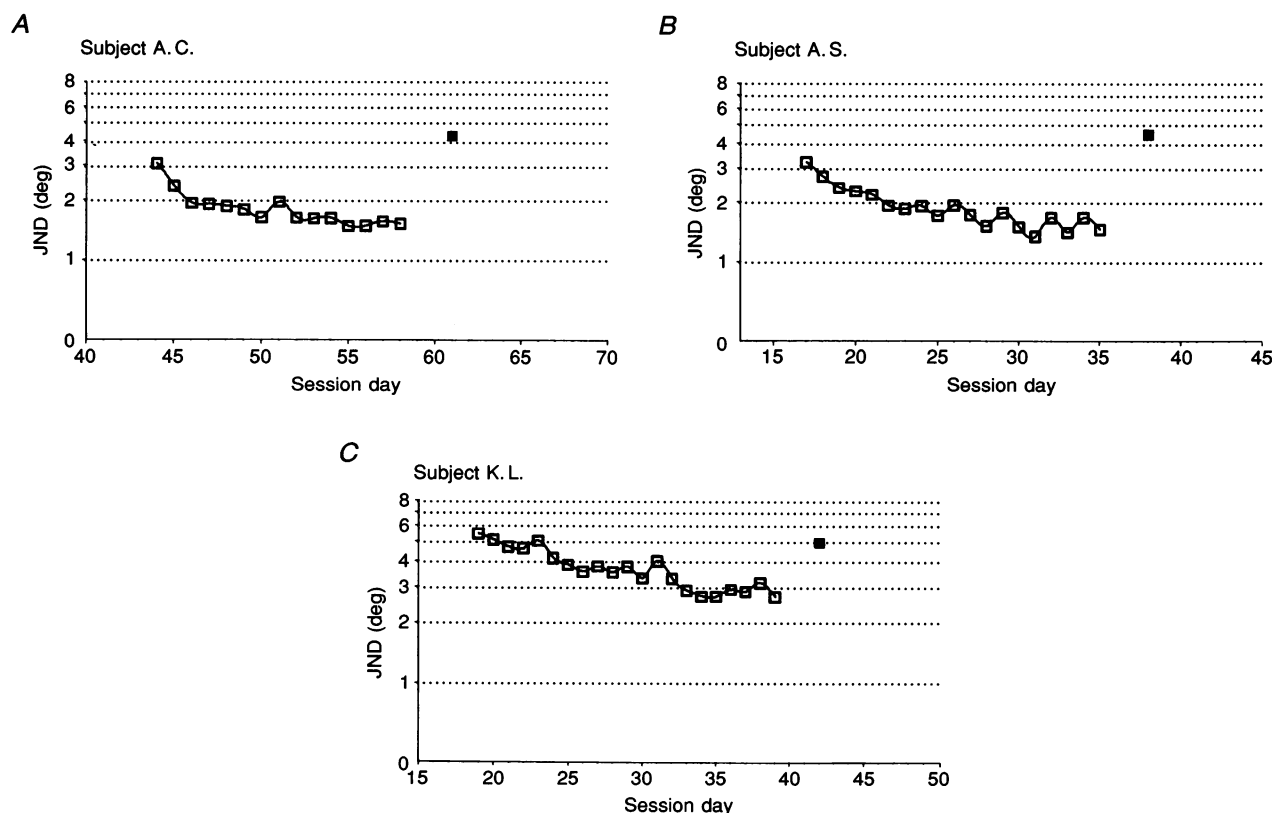


Figure 6. Orientation specificity of the training effect

Three subjects practised orientation discrimination with the staircase method around the left oblique orientation (□, 135 deg), and were then tested on their performance in judging the orientation of the other oblique orientation (■, 45 deg). Stimulus position was at 5 deg eccentricity. Each JND is the median obtained over the whole session, based on 16 blocks of 100 trials. Session numbering does not start from zero, to maintain chronological order for the whole training schedule for each subject. As such, comparison with Figs 2 and 4 is made easier. In *A* and *B*, JNDs for the untrained right oblique orientation were significantly above the pretraining JNDs for the left oblique orientation.

learning curves for the first ten days' sessions at position 1 for subject A.S. Sixteen blocks of 100 trials each were performed each day. The slopes through these sixteen data points were negative, indicating learning, as well as positive, indicating a worsening of performance during the session. For all subjects and for all positions tested, we calculated the slopes per daily sessions. Over the first 10 days, the across-subject ($n = 3$) mean daily slope for a central stimulus, binocularly viewed, was -0.015 ± 0.011 ($n = 30$). The across-subject ($n = 3$) mean for peripheral stimuli, binocularly viewed, was -0.005 ± 0.004 ($n = 77$). Both values are lower than expected: multiplying the slopes by 16 (no. of blocks per day) and by 10 (no. of days) yields a total improvement of 2.40 and 0.80 deg, respectively, markedly lower than the mean total improvement for the first ten days (Table 1, third column), which was 3.68 and 1.18 deg, respectively. With monocular training, where daily sessions consisted of ten blocks, the mean slope or change in JND per block was actually positive: 0.019 ± 0.014 ($n = 40$).

It is possible that when sixteen or even ten blocks of 100 trials are done per day, a build-up of fatigue interferes with performance within the day's session. We therefore split up the sixteen blocks per day into four times four blocks (of 100 trials each block, i.e. a total of 400 trials), and recalculated the slopes through each set of four data points. We chose to split the data this way because Shiu & Pashler (1992) showed improvement in line orientation discrimination within sessions consisting of nine blocks of forty trials each, i.e. a total of 360 trials each session. If only the first four blocks are considered, the across-subject ($n = 3$) mean slope for a peripheral stimulus viewed binocularly was -0.139 ± 0.024 ($n = 77$). In contrast, when considering the next four blocks (block number 5–8), the across-subject mean of the slopes amounted to $+0.009 \pm 0.028$ ($n = 77$). The mean of the slopes if only blocks 9–12 were taken from each session was $+0.017 \pm 0.028$ ($n = 73$), and for the last four blocks it was $+0.031 \pm 0.025$ ($n = 63$). Thus, the change in JND per block becomes more and more positive after the fourth

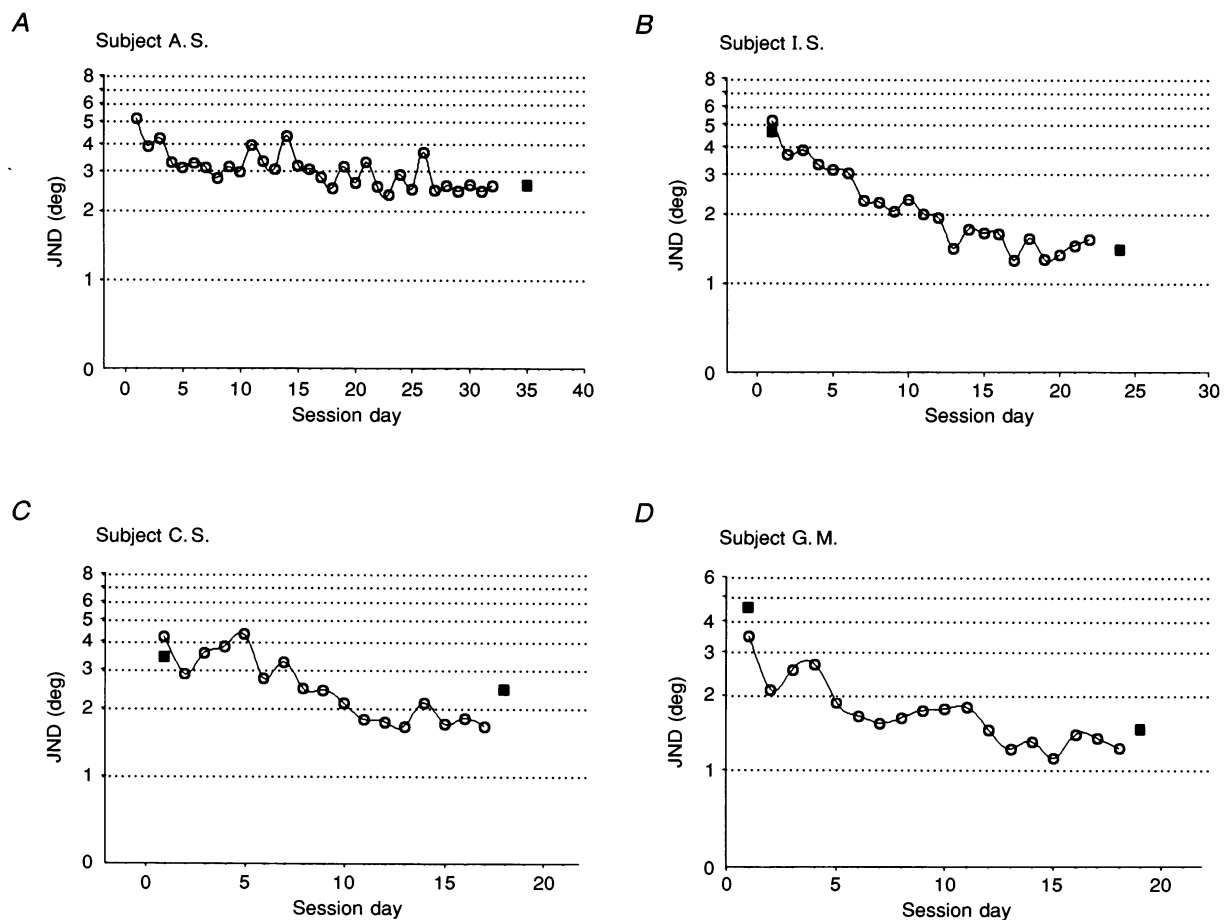


Figure 7. Testing the monocularity of the orientation discrimination learning effect

Four subjects monocularly practised orientation discrimination with the staircase procedure (○, left eye) and were subsequently tested for transfer to the untrained eye (■, right eye). Stimulus position was at 7.9 deg eccentricity (A), 5 deg eccentricity (B and C), and central (D). Each JND is the median obtained over the whole session, based on 10 blocks of 100 trials. Before practising 1 eye, both eyes were tested in 3 of the 4 subjects (5 blocks of 100 trials each).

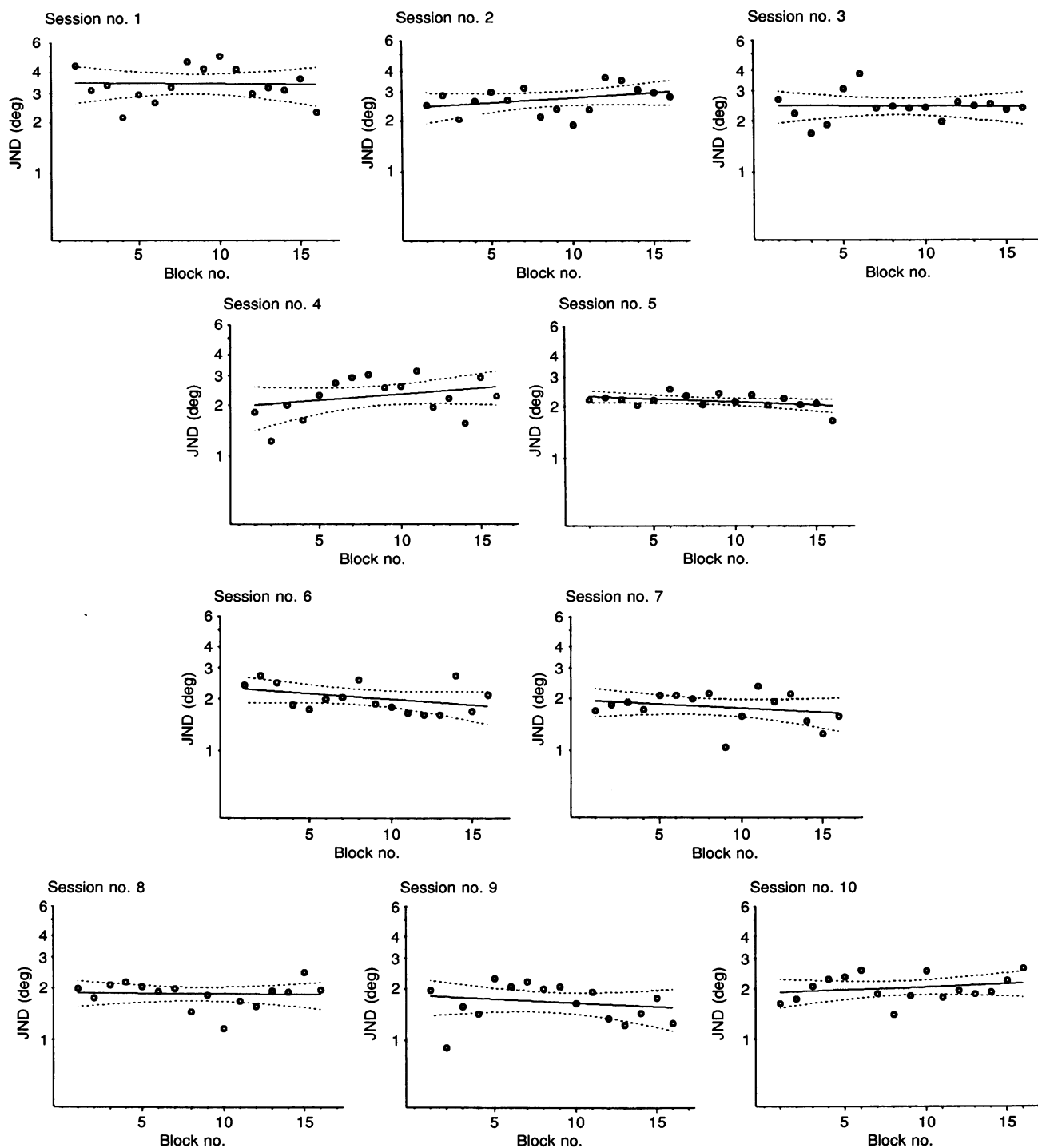


Figure 8. Learning curves per day shown separately, for the first 10 sessions of training subject A.S. at stimulus position 1

Each session represents a different day of practice, and consists of 16 blocks of 100 trials. Shown are linear regression lines and 95% confidence intervals around the lines. Slopes of the regression lines are a measure of the improvement in JND per practice block of 100 trials.

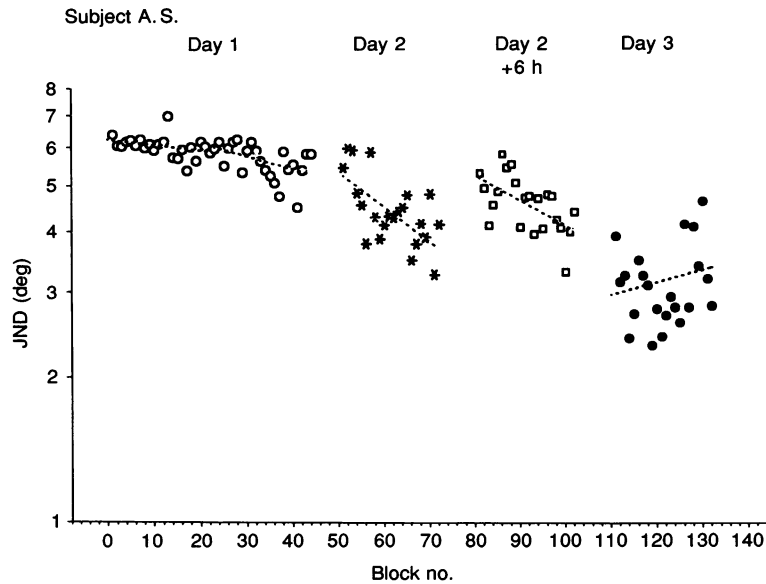


Figure 9. Necessity of a night-long intersession period: three days of learning orientation discrimination

On the first day, the subject (A.S.) practised 44 subsequent blocks of 100 trials each. On the second day, these 44 blocks were split into 2×22 blocks, 6 h apart. On the third day, only 22 blocks were performed. Median JNDs obtained over each 22-block session were 6.03 and 5.705 for the first day, 4.295 and 4.71 for the second day, and 3.03 for the third day. The stimulus was presented centrally and viewed binocularly. Dotted lines are regression lines through each 22-data block.

block, suggesting that fatigue does interfere. Improvement is evident only at the beginning of the daily training schedule.

Other researchers (Karni & Sagi, 1993) have similarly noted the absence of improvement within a daily session, in contrast with clear improvement in performance from one session to the next. They suggested the necessity of a consolidation period of 8–10 h between training sessions for learning to occur. We tested this idea by comparing median JNDs obtained over twenty-two-block sessions, separated from each other by various time periods. Figure 9 shows three different days of training subject A.S. On the first day, forty-four blocks of 100 trials were performed. The next day, twenty-two blocks were presented in the morning, and another twenty-two in the afternoon. On the third day, the subject practised again with twenty-two blocks. Thus, different series of twenty-two blocks were separated by different time periods, zero (or no more than 10 min), 24, 6 and 16 h (including a night). Figure 9 also shows the regression line through each series of twenty-two data points. The median JNDs for each series were 6.03 and 5.705 for the first day, 4.295 and 4.71 for the second day and 3.03 for the third day (Fig. 9). These data indicate that even a time period of 6 h is not sufficient to abolish the effect of fatigue build-up.

Most noticeable is the decrease in JND between different days. Our data suggest that there is a necessity for a latent phase, such as a night's rest, to consolidate the changes that occur as a consequence of practice.

In conclusion, our data indicate that fatigue as well as a consolidation phase play a role in the learning process.

DISCUSSION

The data presented here can be summarized as follows: firstly, human subjects show experience-dependent perceptual improvement in orientation discrimination; and secondly, the characteristics of this form of perceptual learning imply that its neuronal correlates are most probably located early in the visual pathway.

We observed that performance in identification of the oblique orientation could be improved dramatically with practice. Initial thresholds were similar to those reported by others, and higher than reported for vertical or horizontal references (Vogels & Orban, 1985; Matin, Rubsamen & Vannata, 1987), in line with the 'oblique effect' reported for line orientation discrimination and grating contrast sensitivity (Andrews, 1967; Appelle, 1972; Orban *et al.* 1984). Our finding of a dramatic decrease in threshold for the oblique orientation with

practice may not apply to the vertical and horizontal orientation. Since the JND obtained with the MSS is bias-free, the improvement we observed cannot be due to a change in bias, but has to be indicative of an increased sensitivity. It has already been suggested by Vogels & Orban (1985) that the effects of practice upon orientation discrimination originate at the sensory level and not in the decision process, and cannot be attributed to a change in memory noise, attention or accommodation.

Our study elaborated upon these findings to investigate the localization of this form of human perceptual learning in the visual pathway. In order to do so, we studied the position dependency, orientation specificity and eye specificity of the learning effect. After training, a mere displacement of the 2.5 deg diameter stimulus to a new position, such that the trained and new position were next to one another but did not overlap, caused a decrease in performance similar to a displacement as far away as possible without changing the eccentricity. Such a high precision in the retinotopical specificity of the learning effect suggests an early localization, since receptive field size increases sharply as one goes higher up in the hierarchy, and mapping becomes less topographic.

Specificity was also observed for the orientation being trained. Thresholds were even higher after a change in orientation than they were for inexperienced subjects. A similar observation was made in a study on learning Vernier acuity (Fahle & Edelman, 1993), as well as in a study on learning line orientation discrimination (Shiu & Pashler, 1992). This could mean that there is only a limited pool of resources available. In another study on line orientation discrimination (Vogels & Orban, 1985), there was a similar, significant difference between the practised and non-practised orientation. However, in this study, in contrast to our study and that of Fahle & Edelman (1993) and Shiu & Pashler (1992), the threshold for the non-practised orientation had decreased slightly over the training period. It is possible that this decrease was due to their testing of that orientation, not only before training one orientation, but also in the middle of the training. These tests may have been sufficient to initiate changes leading to the improvement for that orientation.

The third aspect of this type of perceptual learning that was studied was the eye specificity of the learning effect. Our results indicate that the mechanism responsible for the perceptual improvement does not remain restricted to monocular cells. Interocular transfer was observed in learning grating spatial phase discrimination (Fiorentini & Berardi, 1981) and motion direction discrimination (Ball & Sekuler, 1987), as in our study. In contrast, absence of interocular transfer was observed in texture discrimination, though only for the slow, between-session

learning, and not for the fast learning that occurs within the training sessions (Karni & Sagi, 1993). Specificity for the trained eye was also observed in hyperacuity training (Fahle, Poggio & Edelman, 1992). However, in hyperacuity tests, accommodation is very important and minor differences between the two eyes can cause significant performance differences.

Where then could the neuronal changes that arose as a consequence of the training reside? The combined specificity of the learning effect for orientation and the position of the noise field in visual space suggest an early localization. In this respect, we have already pointed out the high precision of this position dependency and its relevance. Moreover, the trained stimulus could be positioned as close as 1.6 deg from the vertical meridian, without affecting the other hemifield. These observations certainly exclude V4, V3 and Vp as possible candidates, since in the macaque, receptive field sizes (expressed as the square root of the area) at 5 deg eccentricity are reported to average at least 4.0 deg for V4 (Mountcastle, Motter, Steinmetz & Sestokas, 1987; Gattass, Sousa & Gross, 1988; Boussaoud *et al.* 1991), and 2.5 deg for V3 and Vp (Burkhalter & van Essen, 1986; Gattass *et al.* 1988). These authors also noted a large extent of overlap across the vertical meridian for those areas. In contrast, mean receptive field size values for V2 at 5 deg eccentricity are reported to be less than 2 deg (Gattass, Gross & Sandell, 1981; Burkhalter & van Essen, 1986); mean receptive field sizes for V1 at this eccentricity are reported to vary between 0.3 and 0.8 deg (Dow, Snyder, Vautin & Bauer, 1981; Gattass *et al.* 1981). These quantitative data clearly suggest a localization of the anatomical correlates to the learning effect in V1 or V2. Because of the much larger receptive field size in V2 as compared with V1, together with the relatively small stimulus size and small displacement steps used in our experiments, V1 seems somewhat more likely than V2 as the site of the associated neural changes.

The observation of interocular transfer does not disagree with the suggestion of a localization as early as V1. Even when testing monocularly, binocular cells will be stimulated, and therefore it seems highly unlikely that the learning mechanism would be restricted to monocular cells. Moreover, in the upper layers of V1, monocularity (or strong dominance by one eye) and orientation selectivity seem negatively correlated (Livingstone & Hubel, 1984; Blasdel, 1992). In layer 4, evidence from electrophysiology as well as 2-deoxyglucose and optical imaging studies indicates that in layers 4A and 4Cb, cells are probably exclusively monocular and non-oriented (Blasdel & Fitzpatrick, 1984; Tootell, Hamilton, Silverman & Switkes, 1988), while in layer 4Ca, there are more binocular as well as oriented cells (Blasdel & Fitzpatrick, 1984; Hawken & Parker, 1984; Livingstone &

Hubel, 1984), and 2-deoxyglucose orientation columns (Livingstone & Hubel, 1984) are found. Thus, we can conclude from the interocular transfer only that V1 layers 4A and 4Cb are excluded as the sole locus of the changes accompanying learning.

Finally, it was recently demonstrated that adult primary visual cortex can show a surprising degree of plasticity of topography and receptive field structure (Gilbert & Wiesel, 1992).

Other researchers have recently postulated that learning could well be gated by attention, suggesting the involvement of higher-order visual areas. Firstly, attention appears to be required for performance of the task. Indeed, Sagi & Julesz (1986) and Treisman & Gormican (1988) suggested that discrimination of small orientation differences would demand serial attention. The requirement for attention when performing the task is also indicated by the observation of a decrease in performance caused either by uncertainty regarding the feature to be discriminated (Vogels, Eeckhout & Orban, 1988), or by interference between two orientation discrimination tasks separated in visual space (Duncan, 1984). Secondly, attentional control of the perceptual learning process was demonstrated in two studies (Shiu & Pashler, 1992; Ahissar & Hochstein, 1993). Practising one task did not improve performance in an alternative task, even though both tasks used the same stimuli. This, however, might be not so much an indication of a higher-order localization of the anatomical changes accompanying perceptual learning, but rather that attention could be viewed as gating the information flow, even at early levels. This has been indicated by a recent positron emission tomography study of the human brain during the performance of perceptual tasks (Dupont *et al.* 1993).

As for the nature of the neuronal changes, they remain mostly unknown. That the changes evoked by training must reside in permanently modified neuronal characteristics or in anatomical changes is indicated by the permanent character of the low thresholds. Plasticity studies in the auditory cortex (Recanzone *et al.* 1993) have demonstrated an enlargement of the cortical area activated by the stimuli, as well as more temporally coherent responses across this larger surface. Alternatively, a change in other characteristics of the neurons, such as their orientation tuning bandwidth and their response strength, could be responsible for the sensory improvement. Yet another factor that has not been suggested so far is the development of a better correlation between areas.

Thus, in conclusion, our data indicate that improvement in orientation discrimination evokes a number of changes that are most probably localized early in the visual pathway, where neurons are sensitive to local features

such as orientation of contours at a specific retinal location. Further research, employing electrophysiological and imaging techniques, will be necessary to identify and visualize the changes that must accompany this kind of adult plasticity.

- AHISSAR, M. & HOCHSTEIN, S. (1993). Attentional control of early perceptual learning. *Proceedings of the National Academy of Sciences of the USA* **90**, 5718–5722.
- ANDREWS, D. P. (1967). Perception of contour orientation in the central fovea. Part I: Short lines. *Vision Research* **7**, 975–997.
- APPELLE, S. (1972). Perception and discrimination as a function of stimulus orientation: the 'oblique effect' in man and animals. *Psychological Bulletin* **78**, 266–278.
- BALL, K. & SEKULER, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research* **27**, 953–965.
- BERARDI, N. & FIORENTINI, A. (1987). Interhemispheric transfer of visual information in humans: spatial characteristics. *Journal of Physiology* **384**, 633–647.
- BLAKEMORE, C. & CAMPBELL, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology* **203**, 237–260.
- BLASDEL, G. G. (1992). Differential imaging of ocular dominance and orientation selectivity in monkey striate cortex. *Journal of Neuroscience* **12**, 3115–3138.
- BLASDEL, G. G. & FITZPATRICK, D. (1984). Physiological organization of layer 4 in macaque striate cortex. *Journal of Neuroscience* **4**, 880–895.
- BOUSSAOU, D., DESIMONE, R. & UNGERLEIDER, L. G. (1991). Visual topography of area TEO in the macaque. *Journal of Comparative Neurology* **306**, 554–575.
- BURKHALTER, A. & VAN ESSEN, D. C. (1986). Processing of color, form and disparity information in visual areas Vp and V2 of ventral extrastriate cortex in the macaque monkey. *Journal of Neuroscience* **6**, 2327–2351.
- DOW, B. M., SNYDER, A. Z., VAUTIN, R. G. & BAUER, R. (1981). Magnification factor and receptive field size in foveal striate cortex of the monkey. *Experimental Brain Research* **44**, 213–228.
- DUNCAN, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology General* **113**, 501–517.
- DUPONT, P., ORBAN, G. A., VOGELS, R., BORMANS, G., NUYTS, J., SCHIEPERS, C., DE ROO, M. & MORTELMANS, L. (1993). Different perceptual tasks performed with the same visual stimulus attribute activate different regions of the human brain: a positron emission tomography study. *Proceedings of the National Academy of Sciences of the USA* **90**, 10927–10931.
- FAHLE, M. & EDELMAN, S. (1993). Long-term learning in Vernier acuity: effects of stimulus orientation, range and of feedback. *Vision Research* **33**, 397–412.
- FAHLE, M., POGGIO, T. & EDELMAN, S. (1992). Fast perceptual learning in hyperacuity. *Perception* **21**, suppl. 2, 69.
- FENDICK, M. & WESTHEIMER, G. (1983). Effects of practice and the separation of test targets on foveal and peripheral stereoacuity. *Vision Research* **23**, 145–150.

- FIorentini, A. & BERARDI, N. (1981). Learning in grating waveform discrimination: specificity for orientation and spatial frequency. *Vision Research* **21**, 1149–1158.
- GATTASS, R., GROSS, C. G. & SANDELL, J. H. (1981). Visual topography of V2 in the macaque. *Journal of Comparative Neurology* **201**, 519–539.
- GATTASS, R., SOUSA, A. P. B. & GROSS, C. G. (1988). Visuotopic organization and extent of V3 and V4 of the macaque. *Journal of Neuroscience* **8**, 1831–1845.
- GIBSON, E. J. (1953). Improvement in perceptual judgments as a function of controlled practice or training. *Psychological Bulletin* **50**, 401–431.
- GILBERT, C. D. & WIESEL, T. N. (1992). Receptive field dynamics in adult primary visual cortex. *Nature* **356**, 150–152.
- HAWKEN, M. J. & PARKER, A. J. (1984). Contrast sensitivity and orientation selectivity in lamina IV of the striate cortex of Old World monkeys. *Experimental Brain Research* **54**, 367–372.
- HUBEL, D. H. & WIESEL, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology* **195**, 215–243.
- HUBEL, D. H. & WIESEL, T. N. (1977). Functional architecture of macaque monkey visual cortex. *Proceedings of the Royal Society B* **198**, 1–59.
- KARNI, A. & SAGI, D. (1993). The time course of learning a visual skill. *Nature* **365**, 250–252.
- LIVINGSTONE, M. S. & HUBEL, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience* **4**, 309–356.
- McKEE, S. P. & WESTHEIMER, G. (1978). Improvement in Vernier acuity with practice. *Perception and Psychophysics* **24**, 258–262.
- MATIN, E., RUBSAMEN, C. & VANNATA, D. (1987). Orientation discrimination as a function of orientation and spatial frequency. *Perception and Psychophysics* **41**, 303–307.
- MOUNTCASTLE, V. B., MOTTER, B. C., STEINMETZ, M. A. & SESTOKAS, A. K. (1987). Common and differential effects of attentive fixation on the excitability of parietal and prestriate (V4) cortical visual neurons in the macaque monkey. *Journal of Neuroscience* **7**, 2239–2255.
- ORBAN, G. A., VANDENBUSSCHE, E. & VOGELS, R. (1984). Human orientation discrimination tested with long stimuli. *Vision Research* **24**, 121–128.
- RAMACHANDRAN, V. S. (1976). Learning-like phenomena in stereopsis. *Nature* **262**, 382–384.
- RECANZONE, G. H., SCHREINER, C. E. & MERZENICH, M. M. (1993). Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *Journal of Neuroscience* **13**, 87–103.
- SAGI, D. & JULESZ, B. (1986). Enhanced detection in the aperture of focal attention during simple discrimination tasks. *Nature* **321**, 693–695.
- SCHOUPS, A. A., VOGELS, R. & ORBAN, G. A. (1993). Lack of transfer of perceptual learning in an orientation discrimination task. *Perception* **22**, 123.
- SHIU, L.-P. & PASHLER, H. (1992). Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Perception and Psychophysics* **52**, 582–588.
- TOOTELL, R. B. H., HAMILTON, S. L., SILVERMAN, M. S. & SWITKES, E. (1988). Functional anatomy of macaque striate cortex. I. Ocular dominance, binocular interactions, and baseline conditions. *Journal of Neuroscience* **8**, 1500–1530.
- TREISMAN, A. & GORMICAN, S. (1988). Feature analysis in early vision: evidence from search asymmetries. *Psychological Review* **95**, 15–48.
- VOGELS, R., EECKHOUT, H. & ORBAN, G. A. (1988). The effect of feature uncertainty on spatial discriminations. *Perception* **17**, 565–577.
- VOGELS, R. & ORBAN, G. A. (1985). The effect of practice on the oblique effect in line orientation judgements. *Vision Research* **25**, 1679–1687.
- VOGELS, R. & ORBAN, G. A. (1986). Decision factors affecting line orientation judgements in the method of single stimuli. *Perception and Psychophysics* **40**, 74–84.
- WETHERILL, G. B. & LEVITT, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology* **18**, 1–10.

Acknowledgements

We are grateful to Dr W. Spileers for optometric examinations, to Dr S. Raiguel for help in writing the manuscript, and to P. Kayenbergh and G. Meulemans for technical assistance. We are very much indebted to the volunteer subjects for their goodwill and sometimes enormous amounts of time. This study was funded by an IUAP/PAI project 22, and A.S. is supported by a fellowship from NFWO (National Fund for Scientific Research) Levenslijn No. 7.0008.92.

Received 4 May 1994; accepted 31 August 1994.